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Rieger, J W ; Grüşchow, M ; Heinze, H J ; Fendrich, R

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The appearance of figures seen through a narrow aperture under free viewing conditions: Effects of spontaneous eye motions

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When moving figures are occluded and revealed piecemeal as they move across a narrow slit, observers may perceive them as integrated but distorted. They may also perceive much more of the figure as simultaneously visible than is actually presented at any moment. We obtained quantitative measures of both the perceived distortion and perceived simultaneity under free viewing conditions and related these phenomena to spontaneous pursuit eye movements, the retinal painting produced by this pursuit, and the occurrence of saccades. We found both shape compressions and expansions, depending on figure velocity. We also obtained quantitative evidence that observers perceived slices of the moving figures far wider than the slit through which they were presented. Eye-motion records and retinal stabilization revealed that spontaneous pursuit and the spatially extended images that could have been painted out by this pursuit played no role in the perceived global shape distortions and made only a small contribution to the perceived simultaneity. Therefore, under free viewing conditions, both the distortions and simultaneity of these “anorthoscopic” figure percepts must be the consequence of a postretinal process that integrates the figures over space and time independent of eye motions.

Keywords: shape perception, eye movements, retinal stabilization, aperture, anorthoscopic

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Introduction

Under natural viewing conditions, occluded objects are often revealed in a piecemeal fashion as they move past apertures. Objects revealed in this way are often not only recognized by inference but also perceived as integrated wholes. Even when the aperture is a strait slit that reveals only a narrow slice of a moving object at any moment in time, observers often report seeing the complete object moving across the slit rather than a sequence of local features (Anstis & Atkinson, 1967; Parks, 1965; Zöllner, 1862). These slit-viewed percepts share many of the attributes of simultaneously viewed objects. They can, for example, elicit visual illusions such as the Müller–Lyer illusion (Day & Duffy, 1988; Morgan, Findlay, & Watt, 1982). However, they can also differ from simultaneously viewed objects insofar as they often appear spatially distorted (compressed or elongated). Zöllner (1862)

designated these percepts “anorthoscopic”. He adopted this term from Plateau (1836), who had previously developed a device he termed an “anorthoscope”, which allowed distorted images on a rotating disc to be viewed through a sequence of slits rotating in opposite direction in a manner that allowed them to be seen as undistorted and stationary. It is plausible that Plateau derived the name from the Greek prefixes “ana” and “ortho” to indicate “restoration” of the figures by the viewing device. Whatever Plateau’s intent, following Zöllner, we will use the term anorthoscopic to specifically refer to the integrated percepts formed when an object moves behind a stationary slit.

The visual system must integrate spatial information over time along the motion trajectory of the partially occluded object to form such anorthoscopic object percepts. Observers typically perceive the moving objects compressed along the axis of motion when their velocities are sufficiently high and elongated on the axis of motion

when their velocities are sufficiently low (Anstis & Atkinson, 1967; Helmholtz, 1867; Morgan et al., 1982; Rotschild, 1922; von Vierordt, 1868; Zöllner, 1862). In addition, there is a tendency for observers to substantially overestimate the amount of figure simultaneously visible in the aperture at any moment (Morgan et al., 1982; Parks, 1965; Zöllner, 1862). A review of the early research on anorthoscopic perception can be found in Anstis and Atkinson (1967) and Morgan et al. (1982); a review of contemporary research can be found in Fendrich, Rieger, and Heinze (2005).

Theories seeking to explain the formation of anorthoscopic percepts have sometimes linked their formation, their character, or both to eye movements (Anstis & Atkinson, 1967; Hafed & Krauzlis, 2006; Helmholtz, 1867; Rock, 1981). Alternatively, eye movements observed when observers view anorthoscopic displays (Fendrich et al., 2005; Mack, Fendrich, & Wong, 1982; Morgan et al., 1982) might be contingent on the perception of the motion of the integrated figure.

An eye-motion-based explanation that can, in principle, account for both the formation and properties of anorthoscopic figure percepts is the “retinal painting” hypothesis, which was first formulated by Helmholtz (1867) and continues to be debated (e.g., Anstis, 2005). This hypothesis assumes that observers tend to track the trajectory of a moving object with their eyes as it crosses the narrow aperture, causing a (persisting) image of its successively visible parts to be painted onto adjacent positions on the retina. The resulting spatially extended retinal image is taken to be the basis of the integrated percept of the object. Pursuit that is slower than the actual object velocity will result in a compressed painted image, which could account for the perceived compression of objects that move rapidly. Similarly, pursuit faster than the actual rate of object motion would result in an elongation of the painted image and percept. Finally, the formation of a spatially extended retinal image can account for the apparent increase in the amount of figure that appears to be simultaneously visible. It should be noted, however, that this account of perceived simultaneity depends on both the retinal painting produced by pursuit *and* the persistence of the spatially extended painted image, either at the level of the retina itself or in some subsequent retinotopic store. To acknowledge this, we will henceforward refer to the retinal painting/retinotopic storage hypothesis.

The retinal painting/retinotopic storage hypothesis has an appealing simplicity and has received some empirical support. Specifically, when a continuously visible tracking target is used to guide pursuit eye motions, the image painted by the figure moving behind the slit can be highly predictive of the shape that is perceived (Anstis & Atkinson, 1967; Morgan et al., 1982). Anstis and Atkinson (1967), for example, found that, during the tracking of external targets, the perceived width of a series of ellipses was independent of their actual shape but closely matched

their painted shape. Morgan et al. (1982) found that during the tracking of an external target, when figure velocities were high (10 deg/s) or a very narrow slit was employed (4.5 arcmin), the width of anorthoscopic percepts was reduced proportional to a reduction in retinal painting by partial retinal stabilization, and extended figure percepts were not seen if painting was eliminated by full stabilization. However, with a lower velocity (3 deg/s) and wider slit (9 arcmin), perceived shapes were often wider than the retinal painting/retinotopic storage hypothesis predicted. Moreover, Fendrich et al. (2005), using retinal stabilization, have shown that, under free viewing conditions, anorthoscopic percepts do not require retinal painting with figure velocities of 5 deg/s and slits as narrow as 10 arcmin, and the painting produced by spontaneous pursuit contributes little to the formation and stability of these percepts.

Other accounts of anorthoscopic percepts assume that their construction involves a postretinal process (e.g., a buffer) in which the successively visible object parts are integrated (Morgan et al., 1982; Nishida, 2004; Palmer & Kellman, 2001, 2003; Palmer, Kellman, & Shipley, 2006; Parks, 1965) or that figure percepts are generated by a high-level perceptual “problem-solving” process. To account for the distortions seen in anorthoscopic shapes, it has been proposed that these distortions are a secondary consequence of a misperception of the perceived velocities (Hecht, 1924; Palmer & Kellman, 2001; Rock, 1981), with velocity underestimations leading to apparent compression and velocity overestimations leading to elongation (Rock, 1981). Rock, Halper, DiVita, and Wheeler (1987) have also argued that eye-motion information can serve as an important cue during the derivation of these velocity estimates. Recently, however, Roulston, Self, and Zeki (2006) have proposed a different type of explanation of perceived compressions. The investigators argue that these compressions could be produced by position averaging at a figure’s edges, with the position of a figure’s appearing edge averaged forward in the direction of motion (Fröhlich, 1929) and the position of its disappearing edge averaged backward against the direction of motion.

To the extent that the retinal painting/retinotopic storage hypothesis can be dismissed as an explanation of anorthoscopic percepts under free viewing conditions, the formation of these percepts demonstrates a fundamental process of visual synthesis that entails a temporal binding process that produces percepts of a visually unified world. However, even if the anorthoscopic percepts seen under free viewing conditions are attributable to a process of postretinal visual synthesis, painting could still play a role in determining the phenomenal attributes of the shapes perceived. This could occur because the retinal painting produced by spontaneous pursuit alters the character of the local contour segment information on which the postretinal process operates, so that a distorted shape is derived. Moreover, local retinal painting could serve to

expand the zone of retinal stimulation produced by a figure as its successive parts are revealed through the slit and, thus, contribute the impression of increased figure simultaneity.

It is therefore necessary to determine how eye movements and retinal painting contribute to these characteristics to understand the characteristics of the integrative process that generates anorthoscopic percepts. With the data we report, we address the potential role of the retinal painting produced by spontaneous pursuit on the perceived shape and simultaneity of anorthoscopic figure percepts generated by the postretinal figure-forming process. We do this by obtaining direct measures of both the apparent shape and simultaneity of anorthoscopically viewed shapes under normal free viewing conditions when painting can occur and when painting is eliminated by horizontal retinal stabilization. Our data contribute to the relatively scant quantitative information that is available regarding the magnitude of the figure compressions and expansions that are seen and, to our knowledge, provide the first quantitative measures of the perceived increase in figure simultaneity. Our results indicate that, under free viewing conditions, a figure seen moving behind a narrow slit compresses when its velocity is high and expands when its velocity is low, and these shape distortions occur equally irrespective of retinal painting. We also find that observers have a strong impression of increased figure simultaneity when eye movements cannot produce retinal painting, although painting can contribute to the impression of increased figure simultaneity. Our data also suggest that the amplitude of spontaneous pursuit does not directly affect the shape of figure percepts.

Methods

Apparatus

Displays were generated using a PC and presented on Hewlett Packard 1310A X–Y monitor. This monitor is essentially a large-screen (48 cm diagonal) oscilloscope. The unit we employ has been customized with a P15 phosphor, which has a luminance decay time of 50 μ s to 0.1%. The monitor was driven by 12-bit digital-to-analogue converters on a Data Translation I/O board. Eye motions were monitored with a Fourward Technologies Generation 5 Dual Purkinje image eye tracker, which has a resolution of 1 arcmin. The eye tracker's analogue outputs were sampled with the I/O board's 12-bit analogue-to-digital converters. Subject's responses were obtained with the buttons of a modified computer mouse connected to a digital port on the I/O board. The button responses were sampled at 120 Hz, which was the display refresh rate (see below). A Spectrascan PR650 spectrophotometer with a close-up lens was used to obtain luminance measurements.

Stimuli

Two outline linked-loop shapes were used as the anorthoscopic stimuli. They are shown in [Figures 1A](#) and [1B](#). For convenience, we will refer to them as the *two-loop* and *three-loop* shapes, respectively.

Both shapes were created by summing sinusoidal components with different weightings and frequencies, using an algorithm similar to that used to form traditional Lissajous patterns. They were viewed from a distance of 57 cm and subtended $5^\circ \times 5^\circ$. The shapes were presented through a simulated slit without marked edges; hence, all that was visible to the subject were figure segments that displaced vertically in the slit (see [Figure 1](#)). Each shape was formed from 480 uniformly spaced points, and at the

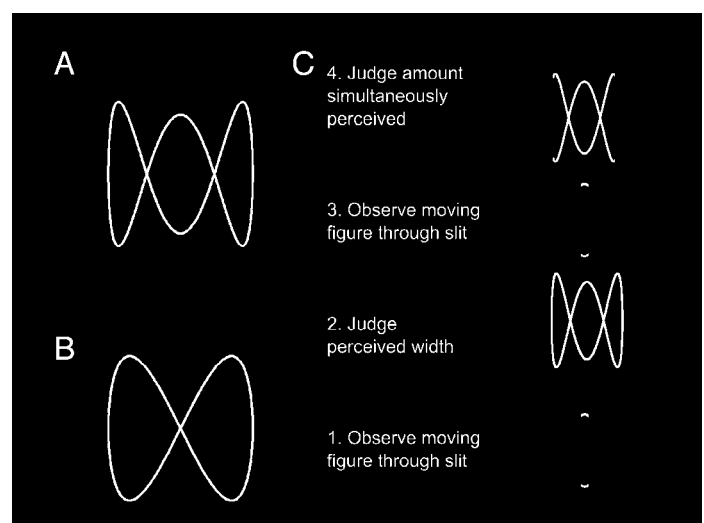


Figure 1. The stimuli and the experimental paradigm. Two outline Lissajous-type figures were used in the experiments: one consisting of three loops (A) and the other consisting of two loops (B). Panel C describes and illustrates the four successive steps in each trial. (1) Each trial started with the presentation of one of the two Lissajous-figures moving horizontally back and forth behind a narrow simulated slit. With these displays, subjects typically report two alternating percepts: line segments as moving vertically up and down or the unified figure moving horizontally behind occluders. Subjects were instructed to judge the width of the integrated figure when it was seen. There were no time constraints. (2) They then switched to the next screen and adjusted the width of a fully visible, static figure to match the width of the figure they had perceived as crossing behind the slit. (3) The figure was then presented moving across the slit a second time, and subjects were instructed to judge the amount of figure they perceived as simultaneously visible. (4) Then, subjects switched to the final display screen and set the width of a static figure cutout to match the amount they had perceived as simultaneously visible when the center of the figure passed through the slit. During this final adjustment, the width of the figure shown matched the width that the subject had reported in Step 2.

subject's viewing distance, they appeared to be drawn with continuous lines. The simulated slit through which the figures were presented had a width of 24 arcmin of visual angle. Pilot investigations indicated that, at this slit, width shape percepts would reliably be seen under stabilized viewing conditions that insured that they were postretinally based. The shapes were advanced behind the simulated slit in steps of 2 or 4 arcmin every 8.33 ms (at 120 Hz), producing an effective horizontal figure velocity of 4 or 8 deg/s and respective figure transit times of 1.25 or 0.625 s. The luminance of the points used to form each figure was 6.0 cd/m², presented against a dark background in a dark room. Shapes initially appeared with their right edge centered in the simulated slit, moved leftward across the slit until their left edge was centered in the slit, and then immediately reversed direction. When seen as integrated shapes, they therefore appeared to be sweeping horizontally back and forth.

Eye-monitoring methods

Subjects viewed stimuli monocularly with their right eye monitored by the Purkinje image eye tracker. A bite plate was used to fix their head position. The eye tracker analogue outputs were initially calibrated by having subjects fixate points in a 4° × 4° grid. Eye position offsets were rezeroed if necessary at the start of each experimental trial. During the experimental runs, the eye tracker's horizontal eye position output was sampled at 120 Hz, just prior to the presentation of each successive figure slice. Displays were horizontally retinally stabilized by using the eye tracker horizontal output to displace the screen position of all the points in the ensuing figure slice so that the simulated slit moved on the display screen in tandem with a subject's horizontal eye movements. The display system allowed for a stabilization accuracy that was limited only by the eye tracker's noise (1 arcmin) and the eye movements that occurred during the interval actually required to display the contour segments making up each figure slice. This interval was generally less than 2 ms. Note that stabilization did not alter the motion of the figure relative to the slit. Horizontal eye-motion records from all trials (both stabilized and nonstabilized) were stored for subsequent analysis. During the experimental trials, a point visible only on an additional monitoring oscilloscope allowed online observation of the subject's eye position, and rare trials in which the tracker did not function correctly were terminated and rerun.

Instruction and procedure

It was explained to subjects that they would be viewing outline geometric shapes through a narrow slit. There were no instructions given regarding pursuit or fixation. The presentation and adjustment sequence the subjects

performed in every trial is outlined in [Figure 1C](#). The trial started with the presentation of the figure moving behind the narrow slit. Subjects were instructed to press a button when they had a clear percept of an integrated shape moving horizontally back and forth and to release this button whenever this percept vanished and they only saw vertically moving line segments. They were told to observe the integrated figure percept when it was present until they had a clear impression of its width and then press a second "go to next step" button with their other hand.

When the "go to next step" button was pressed, the anorthoscopic display was replaced by a complete static comparison figure. This comparison figure was the same as the figure presented as moving behind the slit but was initially set to either half or twice its actual width. Two additional buttons allowed the subject to adjust the horizontal width of the comparison figure so that it matched the width of the figure they had perceived. When they were satisfied with their setting, they pressed the "go to next step" button again, which caused the anorthoscopic display to reappear, with the figure set to its original width moving behind the slit.

The subjects' task was now to judge how much of the figure appeared to be simultaneously visible when it was at the midpoint of its sweep. When they were confident that they could make this judgment, they once again pressed the "go to next step" button. This caused the static comparison figure to reappear, set to the width the subject had adjusted it to. However, only a slice of the comparison figure was shown. This slice was either "wide" (showing the central 90% of the figure), as depicted in [Figure 1C](#), or "narrow" (showing only a 6-arcmin-wide strip of the figure's center). In either case, the subjects used two buttons to widen or narrow the slice until they judged that it matched the appearance of the figure slice they had perceived as simultaneous through the slit. We will refer to this as the subjects' "figure-slice width" setting, with the term "slit width" reserved to denote the physical width of the slit. By using the size-adjusted comparison figure, we hoped to allow subjects to produce the closest possible match to the appearance of the anorthoscopically perceived figure as its center crossed the slit. A final press on the "go to next step" button ended the trial.

Subjects were encouraged to make their judgments based on their actual percepts on each trial, rather than trying to infer the spatial characteristics of the stimulus that had been shown. It was emphasized, in this regard, that when indicating the amount of figure that was seen, they should base their report on the appearance of the figure and not how wide they thought the slit actually was. Each of the two figures was presented four times with retinal stabilization and four times without retinal stabilization at each figure velocity, yielding a total of 32 trials. Each of the four trials with each figure/speed/stabilization combination was coupled with one of the four possible figure-width/slit-size combinations in the adjustment

displays. Trials were run in a unique random order with each subject, with the constraint that there were never more than four successive trials in which the same figure, velocity, or stabilization condition was repeated. Subjects typically completed the full set of 32 trials in about 1 hr. They were given the option of taking a short break when half the trials had been run.

Prior to the start of the main experimental runs, every subject received one to three practice trials with an irregular outline figure that was not used in the later experiment. These trials served to familiarize the subjects with anorthoscopic percepts and experimental procedures. We also ran four trials at the end of the experiment in which subjects were asked to ignore the amount of figure simultaneously seen and, instead, judge the physical slit width. This width was evident when the anorthoscopic figure did not integrate.

Subjects

Sixteen subjects participated in the experiment. Fourteen subjects were undergraduate students at the Otto-von-Guericke University in Magdeburg, Germany. They were paid 6.50 per hour for participating. These subjects were naive with respect to the purpose of the experiment, and none had prior experience with anorthoscopic displays. In addition, two of the authors (J. W. R. and M. G.) participated in the experiment. All subjects gave their informed consent before participating and understood that they could withdraw from the experiment for any reason at any time.

Analysis

The data were analyzed with Matlab R12 (Mathworks Inc.), and statistics were calculated with UnixStat (available from <http://www.acm.org/~perlman/stat/>). After pre-processing to remove saccades and slow drifts, horizontal pursuit eye-motion amplitudes were determined, using a Morlet-wavelet analysis, at the frequency the figure moved back and forth (Torrence & Compo, 1998). The reported amplitudes correspond to the amplitude A in $x(t) = A \times \sin(\omega t)$, where ω represents the sweeping frequency of the figure, t is time, and x is the horizontal position of the eye. Details regarding this method can be found in Fendrich et al. (2005).

Results

Eye movements

In agreement with our previous study (Fendrich et al., 2005), we observed spontaneous pursuit primarily when a

figure percept was reported. Figure 2 illustrates instances of the appearance of pursuit in conjunction with the appearance of a figure percept together with the calculated amplitude of the smooth pursuit. To evaluate the effects of our experimental manipulations on these spontaneous eye movements, we calculated a three-factor ANOVA with factors figure (two levels), velocity (two levels), and stabilization (two levels) on the smooth pursuit tracking amplitudes during the intervals in which subjects reported

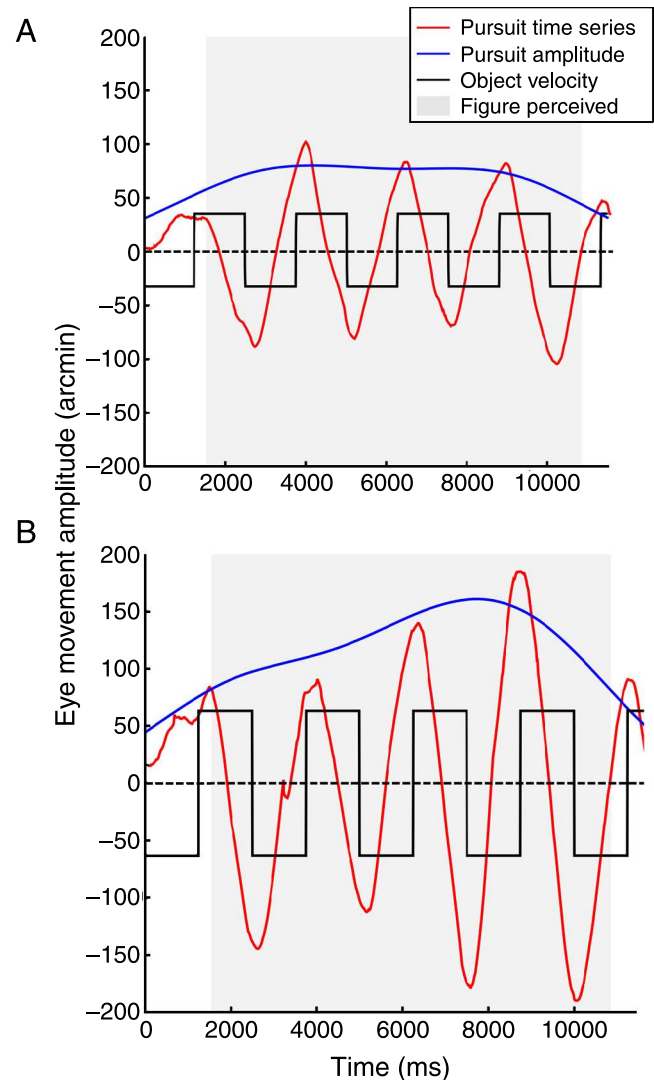


Figure 2. Examples of smooth pursuit eye movements measured while viewing the figures through a narrow slit. The red line indicates the horizontal pursuit component in subject's eye movements after saccades were removed from the time series. The blue line indicates the pursuit amplitude measured with a wavelet analysis. The black square-wave trace shows the reversals in the direction of stimulus movement. Panel A shows pursuit during a nonstabilized trial, and Panel B shows pursuit during a stabilized trial. Gray regions mark the period during which an integrated figure percept was reported. The reversals in the direction of pursuit are phase locked to the reversals in the direction of the stimulus motion.

Figure	Velocity	Stabilization	<i>M</i>	<i>SE</i>
Two-loop	Low	No	59.4	7.2
Two-loop	Low	Yes	114.1	17.7
Two-loop	High	No	37.6	5.37
Two-loop	High	Yes	48.8	9.1
Three-loop	Low	No	65.9	6.7
Three-loop	Low	Yes	123.3	18.0
Three-loop	High	No	37.1	5.8
Three-loop	High	Yes	39.2	8.0

Table 1. Smooth pursuit amplitudes in arc minutes when a figure was perceived during the observation period that preceded the compression settings.

seeing a figure. We found significant main effects of both velocity, $F(1, 15) = 48.3$, $p < .001$, and stabilization, $F(1, 15) = 16.7$, $p < .001$. Increasing the velocity decreased the overall smooth pursuit amplitude (from 90.7 arcmin at low velocity to 40.7 arcmin at high velocity, collapsed across stabilization), and stabilization increased that amplitude (from 50 arcmin [nonstabilized] to 81.3 arcmin [stabilized]). There was no significant main effect of figure, $F(1, 15) = 0.18$, $p > .5$. A significant interaction between velocity and stabilization, $F(1, 15) = 26.1$, $p < .001$, reflected the fact that the effect of stabilization was stronger at low than at high speeds. In addition, a relatively weak interaction effect was found between figure and velocity, $F(1, 15) = 4.8$, $p < .05$: Subjects pursued the three-loop figure slightly more than the two-loop figure at low velocity but slightly less at high velocity. All other interactions were nonsignificant. The smooth pursuit amplitudes for all conditions are listed in Table 1.

Saccades cannot produce a meaningful retinal painting of anorthoscopically viewed figures, but saccadic and perisaccadic effects on perceived spatial stimulus position (Honda, 1991) and motion (Burr, Holt, Johnstone, & Ross, 1982) have been reported (for a review, see, e.g., Ross, Morrone, Goldberg, & Burr, 2001). We wondered if these perisaccadic perceptual distortions contributed to the spatial distortions of the anorthoscopically perceived figures. We therefore also determined the average number of saccades that occurred per figure sweep prior to the subject's figure width adjustment, using a velocity/acceleration saccade detection algorithm. The saccade frequency during the intervals in which subjects reported seeing a figure was compared in a three-factor ANOVA with the factors figure (two levels), velocity (two levels), and stabilization (two levels). We found that subjects produced significantly fewer saccades per stimulus sweep when the slit was stabilized on the retina than when it was fixed on the screen, $F(1, 15) = 19.6$, $p < .001$, presumably because during stabilized viewing, the spontaneous pursuit of the anorthoscopic figure does not result in defoveation of the slit and consequent corrective saccades to refoveate it. In addition, as one might expect from the reduced

sweep duration at high figure velocity, there was also a significant reduction in the number of saccades at high velocity, $F(1, 15) = 86.5$, $p < .001$. The incidence of saccades did not differ for the two figures, $F(1, 15) = 0.3$, $p > .5$. A marginally significant Velocity \times Stabilization interaction occurred, $F(1, 15) = 4.3$, $p = .057$. No other interaction reached significance ($p \geq .099$ in all cases). The exact saccade rates obtained for the different parameter combinations are given in Table 2.

Shape distortions

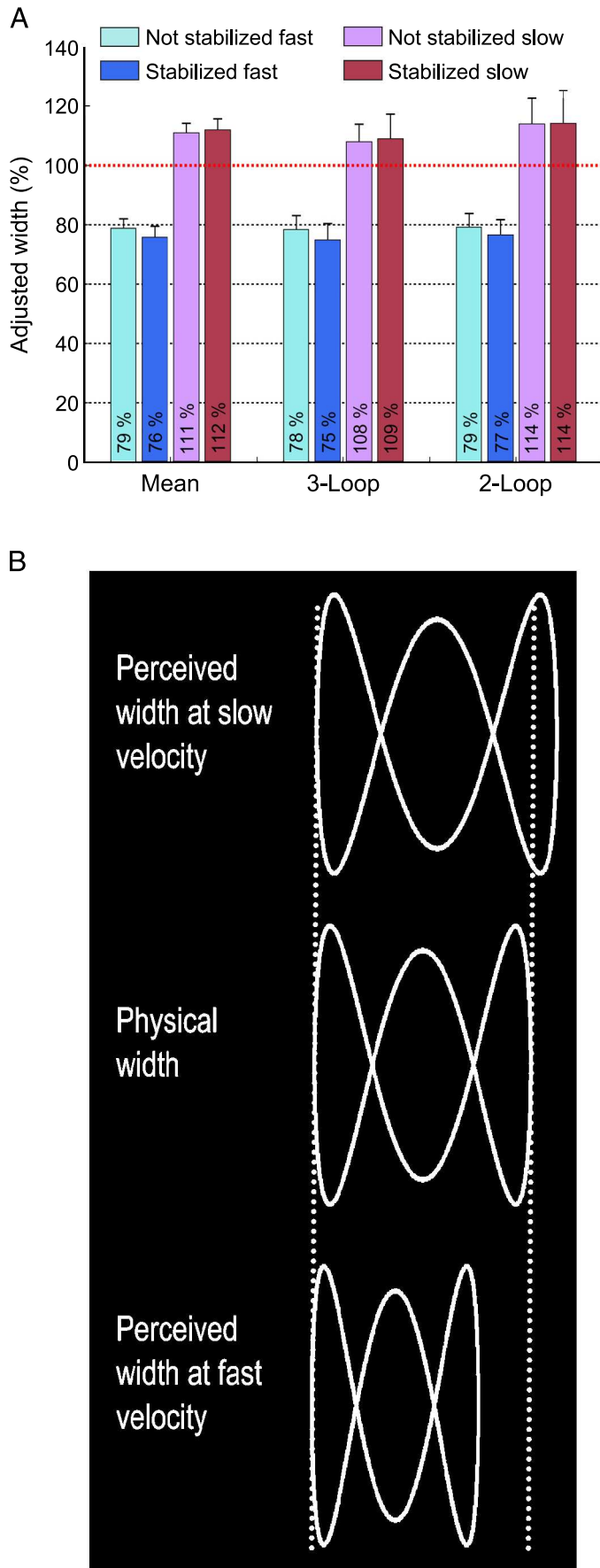
At high velocity, the figures were judged as compressed by an average of 22.7%, and at low figure velocity, figure percepts were expanded by an average of 11%. A three-way within-subject ANOVA with figure type, velocity, and stabilization as factors revealed a highly significant effect of velocity on judged figure width, $F(1, 15) = 31.6$, $p < .001$. There was no significant effect of figure type, $F(1, 15) = 1.3$, $p > .1$, or, critically, retinal stabilization, $F(1, 15) = 0.077$, $p > .1$. In addition, none of the interaction terms reached significance. Because eliminating painting by retinal stabilization had no effect, the data provide no evidence that retinal painting produced by spontaneous pursuit plays any role in the figure compressions or elongations seen under free view conditions. Figure 3A graphs the mean figure width estimates in all the experimental conditions. Figure 3B illustrates the reported appearance of the figures in the high- and low-velocity nonstabilized conditions.

Perceived figure simultaneity

The second property of the figure percept we investigated was the amount of the figure that observers judged to be simultaneously visible. The most straightforward method to obtain an answer for this question from our data is to analyze the absolute width of the figure slice that subjects reported. This measure provides a direct estimate

Figure	Velocity	Stabilization	<i>M</i>	<i>SE</i>
Two-loop	Low	No	1.76	0.21
Two-loop	Low	Yes	1.25	0.23
Two-loop	High	No	0.64	0.12
Two-loop	High	Yes	0.41	0.09
Three-loop	Low	No	1.78	0.17
Three-loop	Low	Yes	1.09	0.18
Three-loop	High	No	0.70	0.11
Three-loop	High	Yes	0.36	0.07

Table 2. Average number of saccades per figure sweep when a figure was perceived during the observation period that preceded the compression settings.



of the apparent width of amount of figure simultaneously seen. This measure can be compared to the width of the slit aperture actually employed. However, this is not a measure of the proportion of the total figure that subjects saw because that will also depend upon the figure compression (i.e., the more a figure is compressed, the greater the proportion that will fit within a slit of a given size). We therefore also report a second measure in which this proportion is estimated.

Absolute figure-slice width

Figure 4A graphs the mean reported figure-slice width in every condition.

A three-way within-subjects ANOVA revealed significant effects of both figure velocity, $F(1, 15) = 6.9$, $p < .05$, and retinal stabilization, $F(1, 15) = 12.1$, $p < .01$. There was no effect of the figure displayed, $F(1, 15) = 0.57$, $p > .1$, and no significant interaction between any of the factors. The actual width of the aperture was 24 arcmin, but (collapsed across stabilization) subjects reported seeing a central figure slice with a mean width of 99.7 arcmin at low figure velocity and a mean width of 80.7 arcmin at high figure velocity. Thus, although the subjects reported seeing a great deal more than was actually presented at both figure velocities, the perceived width of the figure slice was greater when the figure moved more slowly.

The use of retinal stabilization to eliminate retinal painting produced a small but significant reduction in the judged width of the perceived figure slice. With no stabilization, the reported width of the figure slice seen was 109 arcmin at low figure velocity and 88 arcmin at high figure velocity. With stabilization, these widths were reduced to 89.9 and 72.4 arcmin, respectively. This effect argues for a contribution of retinal painting to the width of the figure slice that appeared to be simultaneously visible. However, it is also clear that retinal painting is not the major source of the apparent simultaneity because when painting is eliminated by stabilization, subjects still reported seeing much more of the figure than was ever actually presented at one moment. Figures 4B–4F illustrate the appearance of the figure indicated by the figure-slice width settings and the actual proportion of the figure visible as its center crossed the slit.

Figure 3. The reported compression and expansion of the figures in all viewing conditions. The ordinate in Graph A shows the set width as a percentage of the actual width. Values below 100% reflect perceived compression; values above 100% reflect perceived expansion. Error bars show the standard error of the mean. (B) The actual three-loop figure (center) and its mean judged shape at high (bottom) and low (top) figure velocities. The appearance was virtually identical with and without retinal stabilization (see Panel A).

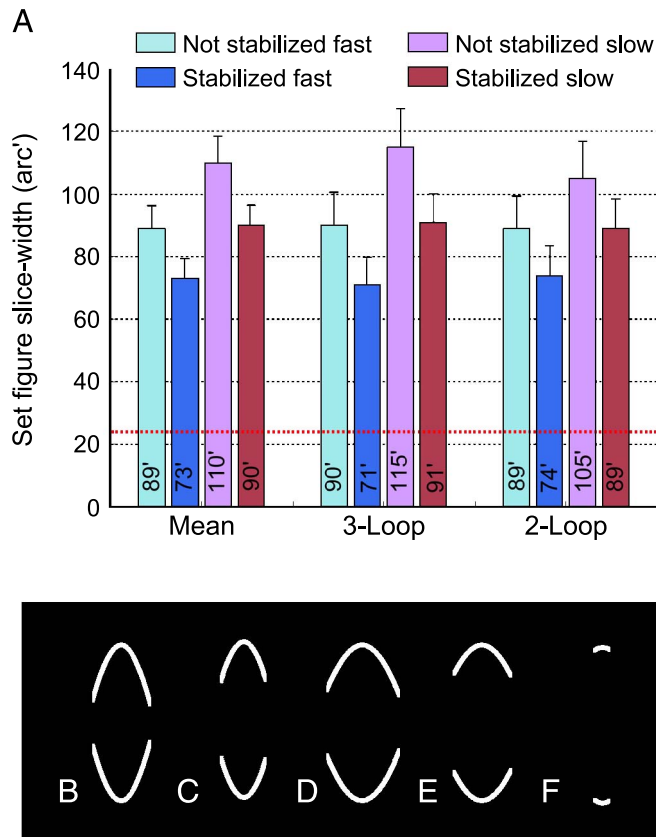


Figure 4. Absolute width of the figure slice reported as simultaneously visible. Graph A shows the cutout width settings in all conditions in arc minutes. In all conditions, subjects set the perceived figure-slice width much larger than the actually presented 24-arcmin slit width (red line). This overestimation was greater at low than at high figure velocity ($p < .05$) and was reduced by stabilization ($p < .01$). Error bars show the standard error of the mean. The lower panel (B–F) illustrates the appearance of the reported three-loop figure slices based on the compression and cutout width settings, as well as the width of the figure cutout actually presented in the slit. (B) Fast non-stabilized, (C) fast stabilized, (D) slow nonstabilized, (E) slow stabilized, (F) actually shown. Results were similar for the two-loop figure (see Panel A).

When subjects were asked to judge the physical width of the slit aperture through which the figures were being displayed rather than the amount of figure that appeared simultaneously visible, they were quite accurate and only slightly overestimated the aperture width (28.9 arcmin; $SE = 1.4$ arcmin).

Proportion of figure seen

We calculated the proportion of the figure that appeared to be simultaneously visible on each trial by dividing the figure-slice width setting by the reported figure compression. For example, if the figure-slice width

setting was 60 arcmin, which would reveal 20% of the undistorted 300-arcmin-wide figure, and the compression was 0.5, so that the figure was reported as half its actual width, the proportion of the figure seen was taken to be 40%. Figure 5 illustrates the resulting mean proportions in all the viewing conditions.

In a three-way repeated measures ANOVA, adjusting for the figure compression in this manner eliminates the significant effect of velocity, $F(1, 15) = 2.4$, $p > .1$. However, stabilization continues to produce a significant reduction in apparent simultaneity, $F(1, 15) = 18.9$, $p < .01$. Once again, figure type does not have a significant effect, $F(1, 15) = 0.5$, $p > .1$, and there are no significant interactions.

In the nonstabilized conditions, subjects reported seeing 37.5% of the figure as its center crossed the slit, averaged across figure type. When stabilization was used to eliminate painting, this value decreased to 31.9%. Because only 8% of each figure was actually visible through the slit, these outcomes support the conclusion drawn from the absolute figure-slice data: Retinal painting can contribute to the apparent simultaneity of anorthoscopically viewed figures, but it is not the primary source of this simultaneity. However, normalizing for the apparent figure shape compensated for the wider figure-slice settings obtained at low figure speed. In fact, despite their wider figure-slice judgments, subjects actually reported seeing a nonsignificantly smaller proportion of the total figure at low velocity (32.1%) than at high velocity (37.3%).

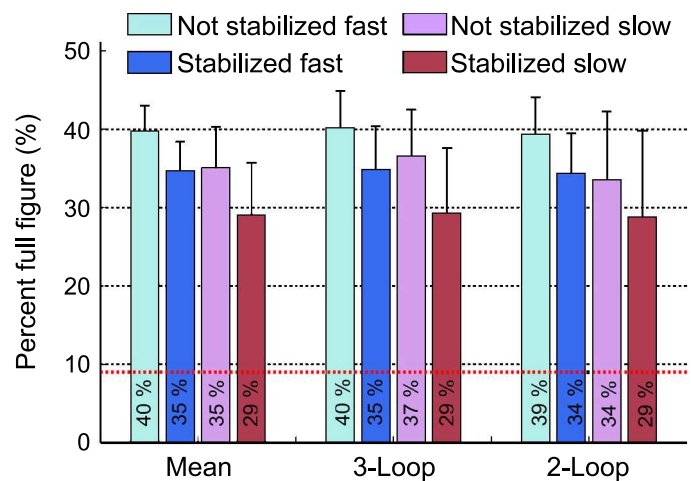


Figure 5. Proportion of figure simultaneously seen. Despite the wider cutout width setting at low figure speed (Figure 4A), the percentage of the full figure reported as simultaneously perceived is similar at low and high speeds. There was even a slight but not significant tendency ($p > .1$) to report a higher percentage of the figure at low speed. The effect of stabilization remains significant ($p < .01$): A smaller percentage of the figure was reported with stabilized viewing. Error bars show the standard error of the mean. The red line shows actual percentage of figure shown (8%).

Discussion

Despite more than 140 years of research, the role of eye motions, retinal painting, and retinotopic storage in the formation of anorthoscopic figure percepts and their role in determining the characteristics of these percepts have remained unclear (Anstis, 2005; Anstis & Atkinson, 1967; Hafeed & Krauzlis, 2006; Helmholtz, 1867; Nishida, 2004; Parks, 1965; Rock, 1981; Shipley & Cunningham, 2001; Zöllner, 1862). There is strong evidence that the deliberate pursuit of an external target can alter the shape of anorthoscopic percepts (Anstis & Atkinson, 1967; Morgan et al., 1982; Rock et al., 1987) and may facilitate the formation of these percepts (Hafeed & Krauzlis, 2006; Helmholtz, 1867), but it is not known whether a similar role is played by the spontaneous eye movements that occur under more natural viewing conditions. Contributing to the difficulty in establishing the functional role of these eye motions, the data regarding them have been scant and largely qualitative in nature.

In this study, we evaluated whether, under free viewing conditions spontaneous eye motions and the retinal painting produced by such eye motions play a role in the perception of the enhanced figure simultaneity and the perceived shape distortions. Our data confirm that, under free viewing conditions, (a) subjects have the strong phenomenal impression that they can see more of these figures than is actually presented through the slit-shaped aperture at any moment and (b) anorthoscopically viewed figures appear to compress at high figure velocities and stretch at low velocities. However, we found that these perceived global shape distortions are not related to either spontaneous pursuit or saccadic eye movements and are unaffected by potential retinal painting due to spontaneous tracking eye-motions. Furthermore, the perception of enhanced figure simultaneity could not be explained by painting into a persisting retinotopic buffer, although painting did serve to slightly enhance this phenomenon. The distortions and apparent simultaneity, therefore, must reflect fundamental properties of figure-forming processes that are largely independent of eye motions under free viewing conditions.

Shape distortions

Morgan et al. (1982) and Shipley and Cunningham (2001) have argued that both retinal painting and a postretinal constructive process of visual object synthesis can mediate anorthoscopic percepts. If figure transit times are rapid and pursuit eye motions are large enough, painting can generate robust figure percepts. When figure transit times are longer and/or pursuit is insufficient, the postretinal process constructs the figure percepts.

When figure percepts are based on painting, perceived distortions can be readily explained by the amplitude of

smooth pursuit (Anstis & Atkinson, 1967; Morgan et al., 1982). Anstis and Atkinson (1967) provided strong support for this account by using the deliberate pursuit of a continuously visible tracking target to control the painting of shapes onto the retina. They found that the painted shapes closely predicted observers' percepts: Pursuit through distances that are smaller than that moved by the figure resulted in compressed percepts; pursuit through distances that are larger than that moved by the figure resulted in expanded percepts, and pursuit in the reverse direction of the moving figure resulted in left–right reversed shape percepts.

However, the deliberate pursuit of a continuously visible moving target will produce a great deal more retinal painting than occurs during the spontaneous pursuit of figures moving behind an narrow slit (Fendrich et al., 2005; Mack et al., 1982; Morgan et al., 1982). Morgan et al. (1982) found that at high figure velocities and with very narrow slits, the formation of a figure percept is not possible without the painting produced by tracking an external target. The dependence on painting with a very narrow slit is understandable if the process that reconstructs the figure shape requires some contour information seen through the slit. As the slit narrows, that information is progressively lost. In the limiting case, the figure behind the slit will be reduced to a set of moving dots that provide no direct contour information. Commensurate with Morgan et al.'s observations, Fendrich et al. (2005) found that, under free viewing conditions, figure percepts were perceived less frequently when the slit size was reduced from 15 to 10 arcmin. However, even with the relatively narrow 10-arcmin slit, intermittent shape percepts were still possible, and these percepts were equally frequent irrespective of whether painting was allowed or eliminated by retinal stabilization. This and other findings led Fendrich et al. to suggest that, under free viewing conditions, the retinal painting produced by spontaneous pursuit contributes little or nothing to the formation of the integrated figure percepts. The present study addresses the question of whether retinal painting nevertheless contributes to the phenomenal appearance of the percepts that occur under these conditions. We found that during free viewing, the perceived figures appear a great deal wider than the shapes predicted by measured spontaneous pursuit. Moreover, when the retinal painting produced by this pursuit was eliminated by retinal stabilization, the perceived shape distortions were unaffected.

Recently, Roulston et al. (2006) proposed a new explanation for the perceived compression of objects moving behind a narrow slit. They suggest that position integration of a moving stimulus over a limited temporal interval (Burr, 1981; Kregelberg & Lappe, 2000) may account for the perceived shape compression. The appearance and disappearance of the elements in the slit are central to their explanation. They propose that the edge of a figure appearing from behind an occluder will be mislocalized forward along the path of motion, whereas a

disappearing edge will be mislocalized backward opposite to the direction of motion. They argue that when shapes are presented through an aperture, the net effect of these combined mislocalizations will be a compression of the figure. However, the applicability of this explanation to the distortions seen in anorthoscopic displays seems questionable. First and most important, it cannot explain the perceived expansion of the figure observed at low figure velocities. Moreover, the shape compression reported by Roulston et al. depends on the spatial motion of the edges of a moving figure across the edges of the aperture. With a narrow-slit anorthoscopic display, this motion will only be unambiguously present at the edges of the figure (with vertical motion otherwise dominant). Thus, the compression effect could only occur at the figure edges and will be limited by the width of the slit. In our experiments, the slit width was 24 arcmin, but we observed a compression that was almost three times this size, and this compression would likely have increased with higher figure speeds.

Shape cueing by eye motions

As an alternative to painting, it has been proposed that the distortions of anorthoscopic figures may be critically dependent on a misperception of their velocity (Hecht, 1924; Palmer & Kellman, 2003; Rock et al., 1987; Shipley & Cunningham, 2001). If a shape is seen as crossing a slit more slowly than it actually is, to account for its passage in a given time, one needs to interpret it as being narrower than it actually is. A similar argument can be made for figure elongations. Commensurate with this view, Rock et al. (1987) have shown that shape distortions in anorthoscopic figures are highly correlated with velocity misperceptions. This raises the question of how observers estimate the velocity of the shape passing behind the slit. Palmer and Kellman (2003) have proposed that the misestimation of velocity occurs in a dynamic representation of the occluded portions of the figure. Rock et al. have argued that eye motions per se could serve as a cue to the velocity of anorthoscopically seen figures and, thus, determine the perceived shape distortions. In support of this argument, they have reported changes in the shape of anorthoscopic figures during the pursuit of external targets under conditions where they argue retinal painting cannot be a source of the percepts. Although they do not directly address the issue of distortions, Hafed and Krauzlis (2006) have made a related suggestion. These investigators propose that corollary discharge signals associated with eye movements may provide a spatial reference frame that permits retinal inputs to be interpreted as a coherent object. However, we found that spontaneous smooth pursuit amplitudes increased under retinal stabilization, but the perceived figure width was unaltered. This casts doubt on the premise that eye-movement signals per se, whether afferent or efferent, necessarily influence perceived shape

of anorthoscopic figures. The same argument can be made for saccades because a significant reduction in the number of saccades during stabilized viewing was not associated with any perceptual change. Thus, perisaccadic distortions of motion, space perception, and time perception (Morrone, Ross, & Burr, 2005; Ross et al., 2001) also do not seem to be a factor in the global shape distortions of anorthoscopically perceived figures.

Spontaneous eye movements, therefore, do not appear to be a good candidate as a general explanation of the perceived distortions of anorthoscopic shapes under free viewing. If these distortions are produced by errors in the estimation of the horizontal speed of the global figure, it appears reasonable to assume that the errors are based on the local motion information provided in the slit. Some figure parts, such as the line crossings, the top and bottom contour arcs, and the vertical contour sections at the edges of the figure, could have provided information about horizontal figure velocity. However, because each of these parts traversed the 24-arcmin slit in less than 50 ms at high velocity and less than 100 ms at low velocity, and because these features differed between our figures but the shape distortion did not, we do not think it likely that they played a critical role in determining the perceived horizontal figure velocity. Alternative sources of information exist. The moving line segments provide at least two sources of motion information for V1 neurons. The line ends signaled vertical motion that could be captured by end-stopped V1 neurons sensitive to motion direction but relatively insensitive to line orientation (Pack, Livingstone, Duffy, & Born, 2003). However, information on both line orientation and line velocity is required to recover the horizontal motion component of the figure. In the intersection-of-constraints theory (Adelson & Movshon, 1982), as well as in the vector-averaging theory (Wilson & Kim, 1994), it is assumed that the velocity components perpendicular to the elements of a moving object are combined at a higher processing stage, presumably area MT (Movshon, Adelson, Gizzi, & Newsome, 1986), to derive the motion of the object. These theories suggest that V1 neurons that combine motion and orientation (Hubel & Wiesel, 1968; Livingstone, 1998) could have provided the critical information for the extraction of the global object motion. However, although mechanisms of this kind can, in principle, explain how the horizontal figure motion could be derived, they do not explain the systematic dependency of the perceived figure width on the physical figure velocity. Our finding that, under free viewing conditions, figures moving behind a narrow slit compress at high velocities and expand at low velocities imposes a constraint on the mechanism that derives the horizontal figure motion. This mechanism would have to allow for both velocity underestimations and overestimations. It has recently been shown that a spatiotemporal energy model of V1 responses predicts interactive dependent variations in speed, size, and orientation (Basole, White, & Fitzpatrick, 2003; Mante &

Carandini, 2005). Such dependencies could provide the neural link between velocity underestimations and overestimations and the deformations of anorthoscopically perceived figures.

Apparent simultaneity

When viewing anorthoscopic displays, observers tend to overestimate the amount of figure simultaneously visible in the aperture at any moment (Morgan et al., 1982; Parks, 1965; Zöllner, 1862). Parks (1965) reported that shapes can, in fact, appear to be completely visually simultaneous. When the rapid painting out of images produces anorthoscopic percepts, visual simultaneity would be readily understandable in terms of persistence in a retinotopic store. However, when (as in our case) anorthoscopic percepts occur in the absence of painting, simultaneity represents a fundamental puzzle. Parks attributed simultaneity to a postretinal storage buffer where images are encoded in terms of their “time of arrival”, translating time into space. Shipley and Cunningham (2001) have made a similar argument. Recently, Palmer et al. (2006) have specifically proposed the existence of a “dynamic visual icon” that can store the shapes of moving occluded objects with position updating for over 300 ms. However, prior to the current experiment, to our knowledge, only qualitative data on the extent of the apparent simultaneity in anorthoscopic displays and its relationship to pursuit eye motions have been reported. In the present experiment, we found strong evidence of simultaneity. We presented 8% (24 arcmin) of our 5° wide figures through the slit, but subjects reported seeing an average of 32% of the figures in the stabilized conditions (in which eye movements produced no retinal painting) and 37% in the nonstabilized conditions (in which eye movements could produce retinal painting). This effect of stabilization was statistically significant. Our data therefore indicate that retinal painting can contribute to the impression of increased simultaneity, but this contribution is small. The mechanism of this small enhancement remains to be clarified, but we think that it is unlikely that painting simply served to add a band of image persistence to an existing figure representation. If that were the case, one would expect the slice of figure perceived during nonstabilized viewing to be asymmetrically extended on its trailing edge. While we did not question our subjects about this, our own phenomenal impressions are that this does not occur: The expanded figure slice appears to be symmetric. This suggests that the small augmentation of perceived simultaneity by painting acts in a uniform manner on all parts of the perceived figure slice.

The data also suggest that observers tended to perceive a similar proportion of the total figure at different figure velocities. Observers reported that the absolute figure-slice width was significantly larger at low figure velocity

than at a higher figure velocity, but when we corrected for the figure expansion and compression to derive the proportion of the figure seen as simultaneous, this proportion was not significantly different at high and low velocities. It therefore appears that the greater judged width of aperture at low figure speed was the result of observers setting the adjustable aperture wide enough to reveal a desired fraction of the figure, and this fraction was similar irrespective of whether the figure was expanded or compressed. This suggests that the process that produces the perception of simultaneity operates subsequent to the stage responsible for the formation of the distorted figure percept because the reported fraction takes the global figure distortion into account.

Conclusions

We conclude that, under the natural free viewing conditions, the phenomenal attributes of the percepts of integrated objects moving behind a narrow slit (anorthoscopic percepts) are based on a postretinal integrative process that is independent of eye motions and painting out the figure into a retinotopic store by spontaneous pursuit. By using retinal stabilization, we show in this study that under these conditions, eye motions and painting do not contribute to perceived shape distortions and contribute very little to the amount of figure observers see at a moment in time. This conclusion is also supported by our previous findings that painting and eye motions do not contribute to the formation and stability of the integrated percepts. Thus, theories that attempt to explain the spatiotemporal integration of moving occluded objects by retinal painting or eye movements are not supported by our results. We suggest that the extraction of local motion information from which estimates of the global figure motion can be derived is critical to the integration process, with cognitive processes serving to resolve the inherent ambiguities in the local motion signals.

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